North American Journal of Fisheries Management 25:1095–1111, 2005

DOI: 10.1577/M04-128.1

[Article]

Validation and Application of a Fish-Based Index of Biotic Integrity for Small Central Minnesota Lakes

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Abstract.—We evaluated the performance of an index of biotic integrity (IBI) based on 16 fish population metrics of three types: species richness, community assemblage, and trophic composition. Two sets of central Minnesota lakes independent from the original set of lakes used to develop the IBI model were used to validate it. One set of lakes (n = 15) had physical features similar to those used to develop the IBI, while the other set (n = 22) averaged 9 m shallower with 28% more littoral area. We used general linear models to test whether the relationships between IBI or individual metric score and indicators of lake quality (trophic state, floristic quality, or surrounding land use) were the same or differed for the original IBI data set and each new data set. Responses were similar among all data sets, lake IBI scores and individual metrics reflecting differences in land use, trophic state, and aquatic habitat. Sensitivity of individual metrics to different measures of stress varied, supporting the need for a multimetric approach when assessing the biotic integrity of lakes. Index of biotic integrity scores were most highly correlated with trophic state (rho = −0.80). Our results support the validity of the original fish-based IBI as a standardized method for quantitatively measuring the condition of fish assemblages and implied overall biotic integrity of small central Minnesota lakes. As with any model, however, continued evaluation is recommended, especially when applying this IBI to lakes with different physical, chemical, or biological characteristics.

Biotic integrity has been defined as the ability of an aquatic ecosystem to support and maintain a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of the natural habitats within a region (Karr and Dudley 1981). The objective of the Clean Water Act (CWA) is to restore and maintain the chemical, physical, and biotic integrity of the waters of the United States. Despite this mandate, a standardized method for assessing the biotic integrity of lake ecosystems has not been developed for Minnesota lakes. Current methods used in Minnesota to address CWA requirements focus on physical and chemical monitoring of lake trophic state and its relationship to swimming and esthetic uses (MNPCA 2002). Current monitoring, however, fails to detect many human-induced perturbations to the biotic integrity of lakes, such as alteration of natural shorelines or invasion by exotic species (Karr 1981, 1994, 1995). In addition, chemical monitoring alone does not reveal changes in organisms exposed to the stressors. Direct assessments of fish assemblages are more relevant to those concerned with fish populations than are surrogate approaches based on other assemblages (such as invertebrates; Mebane et al. 2003) or abiotic criteria alone (Yoder and Rankin 1998). Consequently, a fish-based IBI is critically needed by a fisheries agency such as the Minnesota Department of Natural Resources (MNDNR) charged with protecting fish populations (MNDNR 2004) that generate US$1.28 billion of expenditures on an annual basis (USFWS 2001).

A widely used standardized method for measuring the integrity of aquatic ecosystems is the index of biotic integrity (IBI). Originally developed by Karr (1981) for midwestern streams, this multimetric approach defines a group of measures or metrics that (when combined) reflect the overall biological condition of a water body (Barbour et al. 1995). Metrics comprising an IBI should reflect some aspects of the biological structure, function, or the other measurable characteristic that changes in a predictable manner with increased ecosystem stress (Fausch et al. 1990). The IBI approach has been applied to streams of varying sizes across North America (Fausch et al. 1984; Karr et al. 1986; Miller et al. 1988; Lyons et al. 1995; Lyons et al. 2001; Paller et al. 1996; Hughes et al. 1998; Yoder and Smith 1999; Mebane et al. 2003) and other parts of the world, including Australia, Africa, France, Belgium, and India (Simon and Lyons

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Received July 6, 2004; accepted February 22, 2005
Published online July 22, 2005

TABLE 1.—Standardizing criteria for the 16 metrics used in the fish-based index of biotic integrity (IBI) developed by Drake and Pereira (2002). Calculated scores less than 0 or greater than 10 are constrained to 0 and 10, respectively. The cyprinid metric excludes common carp.

Metric	Code	Standardizing criteria
Species richness metrics		
Native species	NAT	0.4 × number of native species
Intolerant species	INTOL	2.0 × number of intolerant species
Tolerant species	TOL	10 − (3.33 × number of tolerant species)
Insectivore species	INSECT	0.77 × number of insectivore species
Omnivore species	OMNI	12.0 − (2 × number of omnivore species)
Cyprinid species	CYP	2.0 × number of cyprinid species
Small benthic dwellers	SMB	2.5 × number of small benthic-dwelling species
Vegetation dwellers	VEG	1.67 × number of vegetation-dwelling species
Community assemblage metrics based on nearshore relative abundance		
Intolerant individuals	RAINTOL	18.94 × proportion intolerant individuals
Small benthic dwellers	RASMB	109.89 × proportion small benthic-dwelling individuals
Vegetation dwellers	RAVEG	19.84 × proportion vegetation-dwelling individuals
Trophic composition based on trap-net relative biomass		
Insectivore species	BINSECT	12.35 × proportion insectivores by biomass
Omnivore species	BOMNI	10 − (16.39 × proportion omnivores by biomass)
Tolerant species	BTOL	10 − (25.64 × proportion tolerant individuals by biomass)
Trophic composition based on gill-net relative biomass		
Top carnivore species	BTCARN	11.0 × proportion top carnivore species by biomass
Intolerant individuals	BINTOL	125.0 × proportion intolerant individuals by biomass

1995; Hughes and Oberdorff 1998). Thus far, fewer attempts have been made to apply this approach to lentic systems. This is due likely to difficulties classifying lakes into similar groups, predicting fish assemblages for these groups, and sampling issues (Plafkin et al. 1989; Whittier 1999). When it has been applied to lentic systems, success has been mixed (Minns et al. 1994; Harig and Bains 1999; Jennings et al. 1999a; Schulz et al. 1999; Whittier 1999; Lyons et al. 2000; Drake and Pereira 2002).

The fish-based IBI developed by Drake and Pereira (2002) demonstrated potential as a standardized method for assessing the biotic integrity of Minnesota lakes; however, this IBI was not tested on a set of independent lakes. Lakes used to develop this IBI ranged in size from 48 to 200 ha, had similar geophysical and chemical features, and covered a wide range of human-induced disturbances. In contrast to lotic IBIs that typically are based on a single sampling gear (i.e., electrofishing), this IBI required multiple sampling gears (seining, electrofishing, trap nets, and gill nets). This IBI is comprised of 16 metrics of three types: species richness, community assemblage, and trophic composition (Table 1; Drake and Pereira 2002). For these lakes, IBI scores reflected differences in watershed land use, trophic state, and aquatic vegetation.

The goal of this study was to test the performance of the fish-based IBI developed by Drake and Pereira (2002) on an independent set of lakes with features similar to those used to develop the IBI as well as to test IBI performance on a broader range of lake types. To be a valid method for measuring biotic integrity, the IBI developed by Drake and Pereira (2002) must show consistent relationships to lake quality and human-induced stresses in lakes not used to develop the IBI. In addition, the range of lake types over which the application of this IBI is appropriate must be established. As Plafkin et al. (1989) stated, IBI performance is based on expected characteristics of a specific assemblage type, in a specific size and type of water body, in a specific ecoregion or basin. As a result, IBIs must be developed for classes of reasonably comparable lake ecosystems.

Methods

Data sources.—We compiled two new data sets along with the original IBI data set used by Drake and Pereira (2002) to test IBI performance. The first data set comprised 15 lakes that had similar physical and chemical features as the lakes used to develop the IBI (Table 2). We used this data set to verify IBI performance and will refer to it as the validation data set. The second data set comprised 22 lakes from lake-classes with different physical features (shallower and more littoral) but similar surface area (Table 2). We used this data

TABLE 2.—Mean and range of physical and chemical lake characteristics and minor watershed land use for lakes in the original IBI data set, the validation data set, and the range data set. (Sample sizes for alkalinity were 38, 14, and 13, respectively; sample sizes for floristic quality indices were 42, 5, and 12, respectively; and sample sizes for lakeshed area were 28, 9, and 13, respectively.)

	Original (N = 52)		Validation (N = 15)		Range (N = 22)	
Lake characteristic						
Area (ha)	101	(48–180)	136	(57–203)	104	(46–186)
Maximum depth (m)	17	(6–43)	16	(12–24)	8	(4–16)
Littoral area (%)	41	(15–77)	40	(26–69)	69	(37–100)
Shoreline development index	1.6	(1.0–2.9)	1.6	(1.0–2.6)	1.8	(1.1–5.0)
Alkalinity ($CaCO_3$)	120	(35–201)	121	(66–180)	121	(61–185)
Trophic state index	47	(34–69)	48	(30–63)	53	(40–74)
Floristic quality index	23	(8–35)	24	(14–29)	23	(12–28)
Lakeshed area (ha)	931	(229–5,911)	1,065	(184–2,551)	1,370	(283–3,077)
Land use (%)						
Forest	30	(3–74)	24	(0–72)	26	(0–64)
Cultivated	22	(0–68)	32	(6–77)	31	(0–72)
Urban	16	(1–87)	12	(0–62)	4	(0–19)

set to test IBI performance on a broader range of lake types and will refer to it as the range data set. We limited the tests of IBI performance to lakes of similar lake area as the original IBI because species richness is positively related to lake area (Matuszek and Beggs 1988; Minns 1989; Magnuson et al. 1994; Pierce et al. 1994; Alimov 2001; Eadie et al. 1986). Lakes in the original, validation, and range data sets covered a broad range of human-induced degradation, from relatively undisturbed lakes in forested watersheds to highly disturbed lakes in primarily agricultural or urban watersheds. As with the original IBI data set, lakes in the validation and range data sets were located in two ecoregions (the Central Hardwood Forest Ecoregion and the Northern Lakes and Forest Ecoregion [Omernik 1987; Heiskary and Wilson 1989]) and belonged to four major drainage basins (Upper Mississippi River, Red River, St. Croix River, and Minnesota River). All but four species (cisco *Coregonus artedi*, brook silverside *Labidesthes sicculus*, flathead catfish *Pylodictis olivaris*, and mottle sculpin *Cottus bairdii*) collected in the 89 lakes occurred in the four drainage basins (Bell Museum of Natural History 2004).

Sampling.—Fish data were collected using trap nets, gill nets, shoreline seining, and backpack electrofishing following methods described in Drake and Pereira (2002). All fish sampling in each lake occurred during the same year. Eight lakes were sampled in 2001, 15 lakes in 2002, and 14 lakes in 2003. Trap-net and gill-net samples were collected from June through August as part of MNDNR's standardized lake survey program (MNDNR 1993). The number of trap nets and gill nets set depended on lake size; the average was six gill nets and nine trap nets per lake. Net sites were chosen to represent available habitats, such as various depths, points, or bays. Trap nets had a 12.2-m lead approximately 1.1 m deep with two 1.8-m × 0.9-m frames and six 0.76-m hoops with a 13-cm-diameter throat; all mesh was 19-mm bar nylon. Gill nets were 76-m × 1.8-m with six 15.2-m panels of 19-, 25-, 32-, 38-, and 51-mm-bar mesh. Nets were set overnight and emptied the next day. Species were identified, counted, and weighed. Nearshore fish assemblages were sampled using shoreline seining and backpack electrofishing conducted between 20 August and 1 October. The seine was 15.2-m × 1.5 m with a bag, and all mesh was 6.4-mm nylon. In each lake, 10 random but equally spaced 30-m sampling stations were sampled with each gear, alternating which gear was used first. Two shocking passes were conducted at each station, one near the shoreline and one at a depth of approximately 75–100 cm. One 30-m seine haul parallel to the shoreline and out to the length of the seine or to the maximum wadable depth (approximately 1.3 m) was completed. Species were identified and counted. Seining and electrofishing data (nearshore data) were pooled by station, each station representing one unit of sampling effort. In some lakes excessive vegetation, depth, or extremely soft bottom would not permit seining. In these situations, only electrofishing was conducted, if necessary, from a boat.

Metric scoring.—Fish species were classified as to disturbance tolerance (intolerant, neutral, or tolerant), feeding (insectivore, omnivore, or top carnivore), habitat specialist (vegetation dwelling, small benthic dwelling, or other), and family (cyprinid or other) according Drake and Pereira (2002;

Table 3). We classified species not listed in Drake and Pereira (2002) using information from the literature and personal observation. Richness metrics, defined as the number of species within tolerance, feeding, habitat, or family groups, were calculated by combining species presence across all sampling gears. As determined by Drake and Pereira (2002), community assemblage and trophic composition metrics were gear specific. Trap-net data were used to calculate metrics describing the relative biomass of tolerant, insectivore, and omnivore fishes, while gill-net data were used to calculate metrics describing the relative biomass of intolerant and top carnivore fishes. Nearshore data (seine and backpack electrofishing) was used to calculate metrics describing the relative abundance of intolerant, vegetation dwelling, and small benthic dwelling fishes. We used criteria from Drake and Pereira (2002; Table 1) to standardize metrics to values between 0 and 10. The maximum possible lake IBI score was 160.

Measures of human-induced stress and lake habitat.—The Carlson trophic state index (TSI; Carlson 1977) was used as an indicator of cultural eutrophication in a lake as measured by total phosphorus, chlorophyll *a*, and summer Secchi transparency. Trophic state indices were obtained for all 89 lakes from the Minnesota Pollution Control Agency (MNPCA 2004).

The floristic quality index (FQI) was used as an index of habitat. Aquatic plant data were obtained from the MNDNR standardized lake survey sampling (1993), and floristic quality indices were calculated by D. Perleberg (MNDNR, unpublished data) using methods described by Nichols (1999). The FQI combines the conservatism of the species present with a measure of species richness; FQIs were available for 59 lakes.

The Minnesota Land Management Information Center (LMIC 1999) has integrated six different source data sets to provide a generalized overall view of Minnesota's land use. In the LMIC report, land use was reflected by a generalized eight-category legend and data was standardized to 30-m grid cells. Source data sets were collected between 1987 and 1996. The eight land use categories were urban and rural development (Urb), cultivated land (Ag), hay–pasture–grassland (Grass), brushland (Brush), forested (For), water (Wat), bog–marsh–fen (Bog), and mining (Mine).

Coverage of each land use was calculated at three spatial scales: a 100-m buffer around a lake's shoreline, individual lake watershed (lakeshed), and minor watershed. Individual lake watersheds were delineated using height of land delineation techniques. Individual lake watersheds delineations were available for 51 of the 89 lakes used in this study. A minor watershed was defined as an area of at least 12.95 km^2 (1,295 ha) enclosed by a continuous height of land drainage (MNDNR 1999). Minor watersheds and 100-m buffers were available for all lakes.

We classified lakes into different land use groups based on percent forest, cultivated, and urban land use at the minor watershed scale. We chose these land uses because they displayed the greatest variation (Figure 1) and were available for all 89 lakes. We reduced the three land use variables using principal components analysis (PCA) on the correlation matrix (SAS 1999). Then by visual inspection of the plot of principle component 1 against principle component 2, we identified six land use groups. Next, we used general linear models (GLMs; SAS 1999) and Tukey's multiple comparison method to test for differences in land use and lake characteristics among the six land use groups. Principal components analysis was also performed on land use at the 100-m buffer and lakeshed scale. Principal components 1 and 2 for land use in the 100-m buffer (PCA1_BF and PCA2_BF), lakeshed (PCA1_LS and PCA2_LS), and minor watershed (PCA1_MS and PCA1_MS) were used as indices of human-induced disturbance at different scales.

Index of biotic integrity performance.—We tested the performance of the IBI on lakes in the new data sets (validation and range) relative to lakes in the original data set. Using GLMs (SAS 1999), we tested if the relationship between IBI or individual metric scores and indicators of lake quality (TSI, FQI, and PCA1_MS) were the same or differed for the original IBI data set and each new data set. Specifically, we tested whether a model with separate slopes (Weisberg 1985),

$$Y = B_{01} + B_{02} + B_{11}X + B_{12}X + \text{error},$$

fit significantly better than a model with equal slopes,

$$Y = B_{01} + B_{02} + B_{1}X + \text{error},$$

where Y was lake IBI score or individual metric score; X was TSI, FQI, or PCA1_MS; B_{01} and B_{11} were intercept and slope parameters for the original data set; B_{02} and B_{12} were intercept and slope parameters for a test data set; and B_1 was the slope for pooled data.

If slopes were similar for the two data sets, we

TABLE 3.—Family, tolerance, feeding, and habitat classifications for fish species collected in Minnesota lakes by trap nets, gill nets, shoreline seining, and backpack electrofishing. Abbreviations are as follows: I = intolerant, T = tolerant, Fi = filter, He = herbivore, In = insectivore, Om = omnivore, Tc = top carnivore, Smb = small benthic dwelling, Veg = vegetation dwelling. Occurrence is the percent of lakes from the validation (N = 15) and range (N = 22) data sets that included each species.

Species	Family	Tolerance	Feeding	Habitat	Validation data set occurrence (%)	Range data set occurrence (%)	Original data set occurrence (%)
Bowfin *Amia calva*	Amiidae		Tc	Veg	73	55	44
Cisco *Coregonus artedi*	Salmonidae	I	Fi		27	5	21
Rainbow trout *Oncorhynchus mykiss*	Salmonidae		Tc		0	0	2
Central mudminnow *Umbra limi*	Umbridae		In	Veg	20	45	42
Northern pike *Esox lucius*	Esocidae		Tc	Veg	100	91	96
Muskellunge *E. masquinongy*	Esocidae	I	Tc	Veg	13	0	0
Tiger muskellunge (northern pike × muskellunge)	Esocidae		Tc		0	0	10
Common carp *Cyprinus carpio*	Cyprinidae	T	Om		47	55	29
Brassy minnow *Hybognathus hankinsoni*	Cyprinidae		He		0	0	2
Hornyhead chub *Nocomis biguttatus*	Cyprinidae	I	In		0	0	4
Golden shiner *Notemigonus crysoleucas*	Cyprinidae		In		53	55	52
Emerald shiner *Notropis atherinoides*	Cyprinidae		In		0	0	2
Bigmouth shiner *N. dorsalis*	Cyprinidae		In		0	0	2
Pugnose shiner *N. anogenus*	Cyprinidae	I	In	Veg	7	5	0
Blackchin shiner *N. heterodon*	Cyprinidae	I	In	Veg	47	36	37
Blacknose shiner *N. heterolepis*	Cyprinidae	I	In	Veg	47	23	35
Spottail shiner *N. hudsonius*	Cyprinidae		In		20	18	14
Mimic shiner *N. volucellus*	Cyprinidae	I	In	Veg	20	0	17
Spotfin shiner *Cyprinella spiloptera*	Cyprinidae		In		13	18	21
Common shiner *Luxilus cornutus*	Cyprinidae		In		7	9	4
Northern redbelly dace *Phoxinus eos*	Cyprinidae			He	0	0	6
Bluntnose minnow *Pimephales notatus*	Cyprinidae		Om		67	50	75
Fathead minnow *P. promelas*	Cyprinidae	T	Om		13	14	29
Creek chub *Semotilus atromaculatus*	Cyprinidae	T	In		7	14	2
White sucker *Catostomus commersonii*	Catostomidae	T	Om		73	82	73
Bigmouth buffalo *Ictiobus cyprinellus*	Catostomidae		In		0	9	4
Silver redhorse *Moxostoma anisurum*	Catostomidae		In		7	5	0
Shorthead redhorse *M. macrolepidotum*	Catostomidae		In		0	9	4
Greater redhorse *M. valenciennesi*	Catostomidae	I	In		7	5	4
Black bullhead *Ameiurus melas*	Ictaluridae	T	Om		47	86	62
Yellow bullhead *A. natalis*	Ictaluridae		Om		93	95	90
Brown bullhead *A. nebulosus*	Ictaluridae		Om		60	73	50
Tadpole madtom *Noturus gyrinus*	Ictaluridae		In	Smb–Veg	20	41	33
Flathead catfish *Pylodictis olivaris*	Ictaluridae		Tc		0	0	2
Channel catfish *Ictalurus punctatus*	Ictaluridae		Tc		13	9	0
Banded killifish *Fundulus diaphanus*	Fundulidae	I	In		53	45	54
Brook silverside *Labidesthes sicculus*	Atherinopsidae		In		20	9	4
Brook stickleback *Culaea inconstans*	Gasterosteidae		In		7	14	15
Rock bass *Ambloplites rupestris*	Centrarchidae	I	Tc		40	36	33
Green sunfish *Lepomis cyanellus*	Centrarchidae		In		73	73	81
Pumpkinseed *L. gibbosus*	Centrarchidae		In		100	100	92
Bluegill *L. macrochirus*	Centrarchidae		In		100	100	100
Hybrid sunfish *Lepomis* spp.	Centrarchidae		In		67	86	90
Smallmouth bass *Micropterus dolomieu*	Centrarchidae	I	Tc		13	9	12
Largemouth bass *M. salmoides*	Centrarchidae		Tc		100	100	98
White crappie *Pomoxis annularis*	Centrarchidae		Tc		7	5	19
Black crappie *P. nigromaculatus*	Centrarchidae		Tc		100	100	92
Rainbow darter *Etheostoma caeruleum*	Percidae	I	In	Smb	0	0	2
Iowa darter *E. exile*	Percidae	I	In	Smb–Veg	60	64	77
Least darter *E. microperca*	Percidae	I	In	Smb–Veg	0	14	0
Johnny darter *E. nigrum*	Percidae		In	Smb	67	50	65
Blackside darter *Percina maculata*	Percidae		In	Smb	0	5	0
Yellow perch *Perca flavescens*	Percidae		In		100	91	98
Logperch *Percina caprodes*	Percidae		In	Smb	7	5	10
Walleye *Sander vitreus*	Percidae		Tc		73	59	75
Mottled sculpin *Cottus bairdii*	Cottidae	I	In	Smb	7	0	12

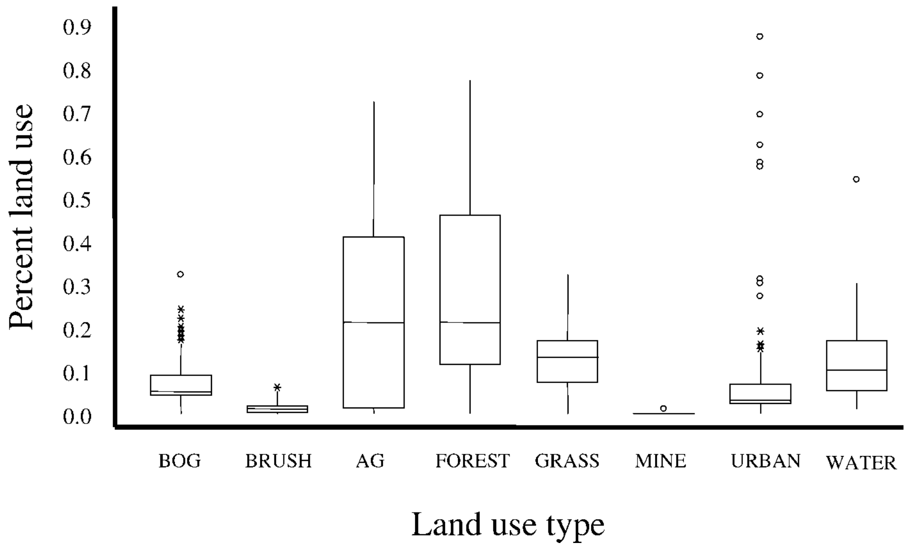

FIGURE 1.—Box-and-whisker plot for percent minor watershed land uses in all 89 lakes. The box encloses the middle half of the data, the line bisecting the box is the median value, the whiskers indicate the range of typical data (not to exceed 1.5 times the size of the box), asterisks indicate possible outliers (values more than 1.5 times the size of the box), and open circles indicate probable outliers (values more than three times the size of the box).

then tested whether the model with separate intercepts fit significantly better than a model with the same intercept, namely,

$$Y = B_0 + B_1X + \text{error},$$

where B_0 and B_1 were intercept and slope parameters for pooled data. The new data set would be considered to support the validity of the original IBI if it had a slope and intercept similar to the original data set.

If a data set (validation or range) displayed a similar relationship between IBI scores and indices of lake quality as the original data set, it was combined with the original data set. The pooled data set was used for further analyses. We used Pearson's correlation and linear regression analysis (SAS 1999) to test for relationships between metric or IBI scores and indices of lake quality. The P-values for the correlations were not adjusted because we did not want to increase type II error and we were interested in the knowledge acquired from each test taken one at a time. We used GLM and Tukey's multiple-range test ($P \leq 0.05$; SAS 1999) to examine the ability of the IBI to predict the assignments of lakes in land use categories. Using linear regression analysis ($P \leq 0.05$; SAS 1999), we tested for relationships between IBI scores and physical lake attributes (such as maximum depth, total area, percent littoral area, shoreline development index [the ratio of the length of the shoreline to the circumference of a circle with the same area as the lake] and lakeshed size) that may influence the impact of human-induced stressors on a lake. The effect of predator stocking on IBI scores was tested with GLM (SAS 1999). Stocking was categorized as none, one species, or mixed (usually two species). A lake was considered stocked if it was stocked more than once during the past 10 years.

Metric contribution to index of biotic integrity score.—Using the pooled data set, we evaluated the relative contribution of each metric to the IBI using methods described by Minns et al. (1994). To do this, we removed a metric from the IBI, calculated a reduced IBI (scaled for the elimination of one metric), and calculated the difference between the reduced and full IBI. This process was repeated for each metric in each lake. Next, for each reduction we calculated the variance of the differences across lakes. The variance of the differences suggests the relative importance of an eliminated metric. High variance of the differences indicates sensitivity of the total IBI to an individual metric. Next, we calculated the variance of the differences across land use groups. The ratio of the variance of differences within a land use group to the variance of the differences across all lakes provides a measure of a metric's range of sensitivity. Metrics with high ratios affect IBI scores in a particular land use group more than metrics with low ratios. Within a land use group, metrics with ratios greater than the group median were considered potentially informative for that group.

Metric variability.—Metric variability was evaluated by examining coefficients of variation (CV, defined as 100·SD/mean) for metrics in least disturbed lakes relative to disturbed lakes. Lakes in the land use group with the greatest percent forest cover (For1) were considered least disturbed. All other lakes were considered disturbed. A high CV among least-disturbed lakes may suggest a metric is too erratic to be relied upon for assessments (Mebane et al. 2003). Metrics with CV values exceeding 100% in least-disturbed waters were often unable to distinguish among streams with varying levels of disturbance (cited in Mebane et al. 2003), whereas a low CV across a range of conditions indicates a metric is unresponsive to changes (Mebane et al. 2003). Metric variability should be higher at disturbed sites due to unstable environmental conditions (Fore et al. 1994).

Results

Sampling

A total of 47 species were collected; 13 were intolerant species and 5 were tolerant species (Table 3). Insectivores were the most common feeding group (29 species), followed by top carnivores (10 species) and omnivores (7 species). Eleven vegetation-dwelling and seven small, benthic-dwelling species were collected. Eleven cyprinid species (excluding common carp *Cyprinus carpio*) were collected. Total species richness averaged 19 species per lake in both data sets (validation and range), and ranged from 13 to 31 in the validation data set and from 12 to 27 species in the range data set. Species composition was similar to the original IBI data set (52 total species; average, 19 species per lake; range, 11–29 species per lake; Drake and Pereira 2002). Most differences in species occurrence among data sets were for rare species that occurred in less than 13% of the lakes in any data set. The most frequently occurring species (>90% of lakes in a data set) across all data sets were bluegill *Lepomis macrochirus*, pumpkinseed *L. gibbosus*, black crappie *Pomoxis nigromaculatus*, largemouth bass *Micropterus salmoides*, northern pike *Esox lucius*, yellow perch *Perca flavescens*, and yellow bullhead *Ameiurus natalis* (Table 3).

Index Validation

The relationship between IBI scores and TSI, FQI, and PCA1_MS was the same for the original and validation data sets (Table 4; Figure 2), supporting the validity of the original IBI. In addition, the relationships were the same for most individual metrics (Table 4). Exceptions included insectivore species richness (INSECT), cyprinid species richness (CYP), small benthic dweller species richness (SMB), the relative abundance of small benthic dwellers in nearshore samples (RASMB), and the relative biomass of omnivores in trap nets (BOMNI), for which a significant slope or intercept difference existed for at least one relationship. Differences for SMB and RASMB could have been due to electrofishing equipment problems experienced during the 2002 field season as electrofishing was the most effective method for collecting small benthic dwelling fishes. Similar to Drake and Pereira (2002) findings, the relative biomass of insectivores in trap nets [BINSECT] was not related to TSI, FQI, or PCA1_MS but was related to percent cultivated land use in the minor watershed (slope test: df = 1, 63, F = 0.08, P = 0.78; intercept test: df = 1, 64, F = 1.81, P = 0.18; pooled data sets: df = 1, 65, F = 9.98, P = 0.006).

Range of Index Performance

The relationship between IBI scores and TSI, FQI, and PCA1_MS was the same for the original and range data sets (Table 4; Figure 2), supporting the validity of using the original IBI on the new lake-classes. In addition, the relationships were the same for most individual metrics (Table 4). Exceptions included vegetative dweller species richness (VEG), SMB, the relative abundance of intolerant fishes in nearshore samples (RAINTOL), RASMB, the relative abundance of vegatation dwellers in nearshore samples (RAVEG), BOMNI, and the relative biomass of intolerant fishes in gill nets (BINTOL) for which a significant slope or intercept difference existed for at least one relationship.

Watershed Land Use

For land use at the minor watershed scale, principal component 1 (PCA1_MS) explained 56% of the variation with inverse loading between forested land use and cultivated land use (Table 5). Principal component 2 (PCA2_MS) explained an additional 40% of the variation with inverse loading between urban land use and forested and cultivated land use. Six land use groups were identified by visual inspection of the plot of the PCA1_MS against PCA2_MS (Figure 3). Land use differed significantly among these groups (Table 6). Lakes in the For1 group were considered least impacted,

TABLE 4.—General linear model results for the performance of the IBI and individual metrics in the validation and range data sets relative to the original data set. IBI or metric responses were measured against lake quality indices that reflected trophic state (TSI), aquatic habitat (FQI), and land use (PCA1_MS). The components reported are lake quality index × data set (for testing separate slopes), data set (for testing separate intercepts), and lake quality index (for testing lake quality effect in the pooled model). Nonsignificant P-values are denoted by ''NS.'' Metric abbreviations are defined in Table 1.

	Original: validation			Original: range		
Metric and df	Slope	Intercept	Pooled	Slope	Intercept	Pooled
TSI						
df	1, 63	1, 64	1, 65	1, 70	1, 71	1, 72
NAT	NS	NS	NS	NS	NS	0.004
INTOL	NS	NS	<0.0001	NS	NS	<0.0001
TOL	NS	NS	<0.0001	NS	NS	<0.0001
INSECT	0.03	NS	0.0007	NS	NS	<0.0001
OMNI	NS	NS	0.002	NS	NS	0.003
CYP	NS	NS	0.007	NS	NS	0.009
SMB	NS	NS	0.02	NS	NS	0.0004
VEG	NS	NS	<0.0001	NS	NS	<0.0001
RAINTOL	NS	NS	<0.0001	0.02	NS	<0.0001
RASMB	NS	0.01	<0.0001	NS	NS	<0.0001
RAVEG	NS	NS	<0.0001	0.04	NS	<0.0001
BINSECT	NS	NS	NS	NS	NS	0.009
BOMNI	NS	NS	0.003	NS	NS	0.0003
BTOL	NS	NS	<0.0001	NS	NS	<0.0001
BTCARN	NS	NS	0.002	NS	NS	0.001
BINTOL	NS	NS	<0.0001	0.04	NS	<0.0001
IBI	NS	NS	<0.0001	NS	NS	<0.0001
FQI						
df	1, 43	1, 44	1, 45	1, 50	1, 51	1, 52
NAT	NS	NS	0.001	NS	NS	0.001
INTOL	NS	NS	<0.0001	NS	NS	<0.0001
TOL	NS	NS	0.002	NS	NS	0.002
INSECT	NS	NS	0.0005	NS	NS	0.0002
OMNI	NS	NS	NS	NS	NS	NS
CYP	0.05	NS	0.11	NS	NS	NS
SMB	NS	0.03	0.03	NS	NS	0.01
VEG	NS	NS	<0.0001	0.03	NS	<0.0001
RAINTOL	NS	NS	0.0004	NS	NS	0.0002
RASMB	NS	0.03	0.02	NS	0.04	0.01
RAVEG	NS	NS	0.002	NS	NS	0.001
BINSECT	NS	0.01	NS	NS	0.02	NS
BOMNI	NS	NS	0.02	NS	0.03	0.03
BTOL	NS	NS	<0.0001	NS	NS	<0.0001
BTCARN	NS	NS	0.0008	NS	NS	0.001
BINTOL	NS	NS	0.04	NS	NS	NS
IBI	NS	NS	<0.0001	NS	NS	<0.0001
PCA1_MS						
df	1, 63	1, 64	1, 65	1, 70	1, 71	1, 72
NAT	NS	NS	0.009	NS	NS	0.002
INTOL	NS	NS	<0.0001	NS	NS	<0.0001
TOL	NS	NS	0.002	NS	NS	0.0005
INSECT	NS	NS	0.008	NS	NS	0.004
OMNI	NS	NS	0.05	NS	NS	NS
CYP	NS	NS	0.03	NS	NS	0.03
SMB	NS	NS	0.0004	0.02	NS	0.002
VEG	NS	NS	<0.0001	NS	NS	0.0003
RAINTOL	NS	NS	0.002	NS	0.03	0.004
RASMB	0.02	0.009	0.008	0.01	NS	<0.0001
RAVEG	NS	NS	<0.0001	NS	NS	NS
BINSECT	NS	NS	NS	NS	NS	0.04
BOMNI	0.03	NS	0.0002	NS	0.03	0.0009
BTOL	NS	NS	0.001	NS	NS	0.003
BTCARN	NS	NS	0.002	NS	NS	0.004
BINTOL	NS	NS	<0.0001	0.003	NS	<0.0001
IBI	NS	NS	<0.0001	NS	NS	<0.0001

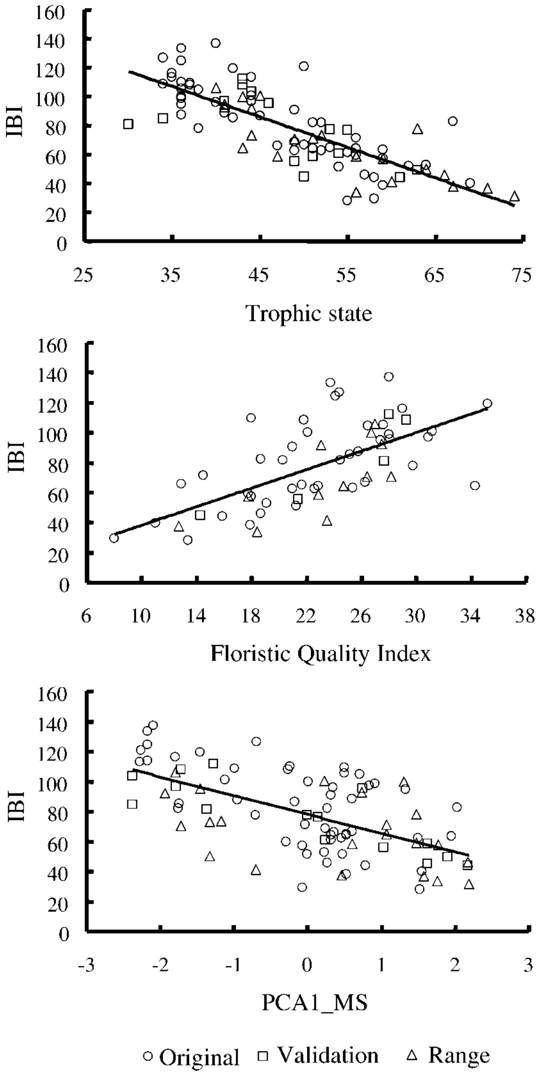

FIGURE 2.—Scatterplot of the index of biotic integrity (IBI) versus trophic state, floristic quality index, and principal component 1 for land use in minor watersheds (PCA1_MS) for the original IBI data set, validation data set, and range data set. The solid line is the linear regression line for all data sets pooled.

having an average of 66% forest cover and less than 4% agricultural or urban activity in their minor watersheds. Lake morphometric indices (area, maximum depth, percent littoral area, and shoreline development index) did not differ among land use groups (Table 6). Mean alkalinity differed among groups as more alkaline lakes were found in agricultural watersheds. At the lakeshed scale, principal component 1 (PCA1_LS) explained 63% of the variation (inverse loading between forested land use and cultivated land use); principal component 2 (PCA2_LS) explained an additional 36% of the variation (inverse loading between urban land use and cultivated land use; Table 5). At the 100-m buffer scale, principal component 1 (PCA1_BF) explained 47% of the variation with inverse loading between forested land use and urban land use; principal component 2 (PCA2_BF) explained an additional 38% of the variation with inverse loading between urban land use and cultivated land use (Table 5).

Capacity to Distinguish Varying Levels of Biological Condition

Given the similarity of IBI performance relative to TSI, FQI, and PCA1_MS among all data sets, we pooled the data for all other analyses. The mean IBI for all lakes was 79 (scores ranged from 28 to 137). Lake IBIs were significantly related to trophic state (Linear regression: R^2 = 0.63, df = 1, 87, F = 149.1, P < 0.0001; Figure 2), floristic quality (Linear regression: R^2 = 0.41, df = 1, 57, F = 39.5, P < 0.0001; Figure 2), and PCA1_MS (Linear regression: R^2 = 0.37, df = 1, 87, F = 50.1, P < 0.0001; Figure 2), scores decreasing as trophic state and cultivated land use increased and floristic quality declined. Metric and IBI scores differed among land use groups (Table 7; Figure 4). IBI scores followed a disturbance gradient in which lakes in the most forested watersheds (For1) had the highest scores, and lakes in primarily agricultural watersheds (Ag) had the lowest scores. IBI scores tended to decrease as either agricultural or urban land use increased in the watershed. Pearson correlation analyses on lake quality indices and metrics and the IBI for all data pooled reinforced earlier findings of Drake and Pereira (2002) as all metrics and the IBI correlated with at least one index of lake quality (Table 8). In general, metrics were most strongly correlated with TSI. Metrics based on vegetation-dwelling species were correlated with FQI. Intolerant- or tolerant-based metrics displayed the strongest correlations with all indices of lake quality. Correlations were similar for PCA1_MS and PCA1_LS as both reflected inversed loading between forested land use and cultivated land use. PCA1_BF, reflecting inverse loading between forested land use and urban land use, was less strongly correlated with metric scores than land use at either the lakeshed or minor watershed scales. The second principal component for land use at any scale was correlated with few metrics. The IBI was most strongly correlated with TSI.

TABLE 5.—Results of principal components analysis on land use variables for all study lakes at three spatial scales (minor watershed, lakeshed, and 100-m buffer).

Principal component	Eigenvalue	Proportion of variance explained	Cumulative variance explained	Coefficient eigenvectors		
				Forested (%)	Urban (%)	Cultivated (%)
Minor watershed (N = 89)						
PCA1_MS	1.69	0.56	0.56	−0.72	0.07	0.69
PCA2_MS	1.21	0.40	0.97	−0.26	0.90	−0.36
PCA3_MS	0.10	0.03	1.00	0.64	0.44	0.63
Lakeshed (N = 51)						
PCA1_LS	1.89	0.63	0.63	−0.71	0.20	0.67
PCA2_LS	1.03	0.36	0.98	−0.05	0.94	−0.33
PCA3_LS	0.07	0.02	1.00	0.70	0.27	0.66
Buffer (N = 89)						
PCA1_BF	1.40	0.47	0.47	−0.75	0.60	0.29
PCA2_BF	1.14	0.38	0.85	−0.12	−0.55	0.83
PCA3_BF	0.47	0.16	1.00	0.65	0.59	0.49

Metric Sensitivity and Variability

The CV for metrics in the least disturbed lakes (For1) ranged from 20% to 105%, while the CVs for metrics in disturbed lakes ranged from 17% to 256% (Table 9). Except for native species richness [NAT], INSECT, and CYP, CVs for metrics in the least-disturbed lakes were lower than CVs for metrics in the disturbed lakes. For these metrics, CVs were similar between least-disturbed and disturbed lakes.

The variance of the differences between full IBIs and reduced IBIs ranged from 2.75 when INSECT was removed to 8.24 when the CYP was removed. The median variance of the differences was 6.67 (Table 10). Variances of the differences were greater than the median when metrics describing intolerant species richness [INTOL], CYP, RAVEG, the relative biomass of tolerant fishes in trap nets [BTOL], BINSECT, BOMNI, and BINTOL were eliminated from the IBI. Sensitivity of the IBI to individual metrics differed among the six watershed land use groups. IBI scores within most land use groups were sensitive to at least one habitat specialist metric. In general, IBI scores for lakes in less-disturbed land use groups (For1, moderately forested watersheds [For2], ForAg) were more sensitive to metrics describing RAINTOL, RASMB, RAVEG, and BINTOL than lakes in the more agricultural and urban land use groups. In contrast, IBI scores for lakes in more disturbed land use groups (AgUrbFor, Urban, and Ag) were more sensitive to metrics describing the relative biomass of top carnivores in gill nets [BTCARN] and BTOL compared with lakes in less disturbed watersheds.

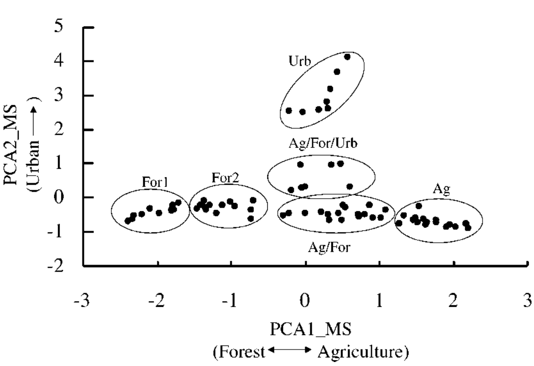

FIGURE 3.—Plot of principal component 1 for land use in minor watersheds (PCA 1_MS) versus principal component 2 (PCA 2_MS). Each oval represents a watershed land use group. See text for abbreviations.

Influence of Natural Lake Characteristics, Ecoregion, and Stocking

Lake IBI scores were not related to alkalinity (linear regression analysis: R^2 = 0.01; df = 1, 63; F = 0.52; P = 0.47), lake area (R^2 = 0.002; df = 1, 87; F = 0.17; P = 0.68), shoreline development index (R^2 = 0.01; df = 1, 87; F = 0.94; P = 0.34), or lakeshed area (R^2 = 0.05; df = 1, 49; F = 2.79; P = 0.10). Lake IBI scores were negatively related to percent littoral area (R^2 = 0.24; df = 1, 87; F = 26.8; $P < 0.001$) and positively related to maximum depth (R^2 = 0.30; df = 1, 87; F = 36.61; $P < 0.0001$). In general, IBIs for lakes in the Northern Lakes and Forest (NLF) ecoregion (mean, 101) were greater than IBIs for lakes in the Central Hardwood Forest (CHF) ecoregion (mean, 68; GLM: df = 1, 87, F = 41.9, $P < 0.0001$).

TABLE 6.—Comparisons of mean lake characteristics and minor watershed land use among the six watershed land use groups. The reported *P*-value is for the full general linear model. Within rows, means with the same lowercase letter are not significantly different (Tukey's multiple range test: $P \leq 0.05$). See text for land use group abbreviations.

Variable	Watershed land use group						df	*F*	*P*
	For1	For2	ForAg	AgUrbFor	Urb	Ag			
Lake characteristic									
Area (ha)	124	112	104	106	111	94	5, 83	1.02	0.41
Maximum depth (m)	17.7	14.3	14.4	16.9	14.8	11.8	5, 83	1.33	0.26
Littoral area (%)	39	51	47	45	47	56	5, 83	1.42	0.23
Alkalinity (mg/L $CaCO_3$)	113 z	93 z	122 zy	113 zy	113 zy	154 y	5, 59	4.37	0.002
Shoreline development index	1.9	1.6	1.6	1.5	1.5	1.6	5, 83	0.92	0.47
Trophic state index	42 z	43 zy	47 zyx	51 yxw	55 xw	58 w	5, 83	9.19	<0.0001
Minor watershed land use									
Forested (%)	66 z	44 y	22 x	22 x	12 w	9 w	5, 83	213	<0.0001
Cultivated (%)	<1 z	4 z	36 y	23 x	4 z	60 w	5, 83	261	<0.0001
Urban (%)	4 z	2 z	4 z	21 y	66 x	4 z	5, 83	327	<0.0001
N	16	14	21	11	9	18			

Lake IBI scores differed significantly among lakes stocked with zero, one, or two predator species (GLM: df = 2, 86; $F = 5.16$; $P = 0.008$). Lakes stocked with two predator species had an average IBI of 58 compared with lakes stocked with zero or one predator species, which each had an average IBI of 82 (Tukey's multiple-comparison test: $P \leq 0.05$). The percentage of lakes stocked with zero (27–36%), one (45–56%), or two (15–20%) species was similar across all data sets.

Discussion

The fish-based lake IBI developed by Drake and Pereira (2002) reflected the relative biotic integrity of a broad array of small central Minnesota lakes. Overall, IBIs for lakes similar to those used to develop the IBI as well as shallower, more littoral lakes had responses to lake quality similar to those for lakes used to develop the IBI. Metrics comprising the IBI had detectable, consistent, and predictable responses to differences in trophic state, land use, and aquatic vegetation. These results support the validity of the fish-based IBI as a standardized method for quantitatively measuring fish assemblages for use in assessing the biotic integrity of small central Minnesota lakes.

Various human activities can directly or indirectly impact lake ecosystems; however, the strong

TABLE 7.—Summary of results from general linear model analysis of metric scores by land use group. Within rows, means with the same lowercase letter are not significantly different (Tukey's multiple range test: $P \leq 0.05$). Metric abbreviations are defined in Table 1; see text for land use group abbreviations.

Metric	Watershed land use group						F^a	*P*
	For1 (*N* = 16)	For2 (*N* = 14)	ForAg (*N* = 21)	AgUrbFor (*N* = 11)	Urb (*N* = 9)	Ag (*N* = 18)		
NAT	8.23	7.71	7.43	6.76	7.47	7.08	2.06	0.08
INTOL	9.00 z	6.86 z	6.19 zy	3.45 yx	2.67 x	2.89 x	10.90	<0.0001
TOL	5.63 z	4.77 zy	3.34 zyx	2.73 zyx	0.38 x	2.23 yx	5.48	0.0002
INSECT	8.08	7.50	7.66	6.51	6.50	6.76	2.25	0.06
OMNI	5.13 z	3.43 zy	3.71 zy	3.45 zy	1.56 y	3.33 zy	2.48	0.04
CYP	5.88	6.29	6.1	5.09	6.00	4.11	1.62	0.16
SMB	7.03 z	4.82 zy	3.45 y	3.64 y	3.61 y	4.86 zy	4.12	0.002
VEG	8.34 z	7.87 zy	6.68 zyx	5.46 zy	4.64 x	5.00 x	5.54	0.0002
RAINTOL	3.87 z	3.09 zy	4.00 z	1.30 zy	0.57 y	0.60 y	5.27	0.0003
RASMB	4.53 z	4.06 zy	1.68 zy	1.98 zy	2.37 zy	1.2 y	4.17	0.002
RAVEG	2.76 zy	2.73 zy	3.44 z	0.67 zy	0.18 y	1.21 zy	3.04	0.01
BINSECT	5.13 zy	5.24 zy	4.85 zy	6.80 z	7.02 z	2.83 y	4.91	0.0005
BOMNI	7.89 z	6.52 z	5.46 zy	6.15 z	6.91 z	2.77 y	6.07	<0.0001
BTOL	9.40 z	8.28 zy	7.66 zy	6.81 zy	6.28 zy	4.65 y	4.13	0.002
BTCARN	8.69 z	7.89 zy	6.92 zy	6.77 zy	6.60 zy	6.15 y	2.92	0.02
BINTOL	5.79 z	2.05 y	1.02 y	0.07 y	0.32 y	0.61 y	9.74	<0.0001
IBI	105.37 z	89.08 zy	79.70 y	67.67 yx	63.07 yx	56.12 x	11.1	<0.0001

[a] df = 5, 83.

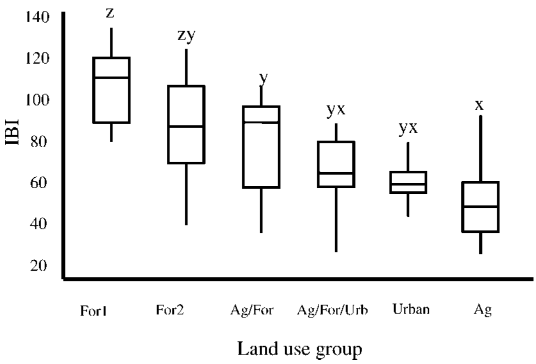

FIGURE 4.—Box-and-whisker plots of index of biotic integrity (IBI) scores for lakes in the six watershed land use groups. The box encloses the middle half of the data, the line bisecting the box is the median value, the whiskers indicate the range of typical data (not to exceed 1.5 times the size of the box), asterisks indicate possible outliers (values more than 1.5 times the size of the box), and open circles indicate probable outliers (values more than three times the size of the box). See text for abbreviations. Mean scores of watershed land use groups denoted by the same lowercase letter were not significantly different ($P < 0.05$) according to general linear models and Tukey's multiple-comparison test.

relationship between IBIs and trophic state suggest cultural eutrophication is an important contributor to the declining biotic integrity of lakes. Carpenter et al. (1998) concluded eutrophication is a widespread problem in river, lakes, estuaries, and coastal oceans, caused by overenrichment with phosphorus (P) and nitrogen (N). Furthermore, they cite nonpoint pollution, primarily from agriculture and urban activity, as a major source of P and N. The trophic state index is a relative index of the levels of nutrients (such as nitrogen and phosphorus) and algae in the lake water (Carlson 1977). In this study, trophic state differed among land use groups, and lakes associated with more agriculture or urban activity had higher TSIs. Adverse effects on lakes by eutrophication are numerous (Smith 1998). The most obvious consequence is increased growth of algae and aquatic macrophytes. Habitat loss can occur as turbidity from phytoplankton, dead material, and inorganic particles increases, shading out macrophytes or confining macrophytes to shallow areas of the lake. In addition, oxygen shortages can occur caused by the senescence and decomposition of both algae and macrophytes. In this study, TSI was negatively correlated with the floristic quality index (Pearson's correlation: N = 59; rho = −0.62; $P < 0.0001$), suggesting a reduction in the complexity of the aquatic plant community in more eutrophic lakes.

Unlike Drake and Pereira (2002), we found a significant difference in the mean IBI score of lakes stocked with two predator species compared with lakes stocked with either zero or one predator species. However, the mean IBI of lakes in the original IBI data set that were stocked with two species also tended to be lower, but not significantly lower. It is not known, however, if this is because of an effect of the stocked predators on the fish community measured by the IBI or the

TABLE 8.—Pearson correlation coefficients between metrics and IBI and trophic state (TSI), floristic quality index (FQI), and principal components 1 and 2 (PCA1 and PCA2) for land use at three scales (minor watershed, lakeshed, and 100-m buffer). P-values are in parentheses (correlations with $P > 0.05$ are denoted by "NS"). Metric abbreviations are defined in Table 1.

			Minor watershed (N = 89)	
Metric	TSI	FQI	PCA1_MS	PCA2_MS
NATIVE	−0.25 (0.02)	0.46 (0.0003)	0.29 (0.006)	−0.04 NS
INTOL	−0.76 (<0.0001)	0.63 (<0.0001)	−0.53 (<0.0001)	−0.28 (0.008)
TOL	−0.55 (<0.0001)	0.44 (0.0005)	−0.38 (0.0002)	−0.30 (0.005)
INSECT	−0.38 (0.0003)	0.48 (0.0001)	−0.26 (0.01)	−0.20 (0.05)
OMNI	−0.35 (0.0008)	0.12 NS	0.20 NS	−0.27 (0.01)
CYP	−0.26 (0.01)	0.12 NS	−0.23 (0.03)	0.06 NS
SMB	−0.31 (0.003)	0.32 (0.01)	−0.30 (0.004)	−0.18 NS
VEG	−0.56 (<0.0001)	0.62 (<0.0001)	−0.41 (0.0001)	−0.24 (0.03)
RAINTOL	−0.62 (<0.0001)	0.49 (<0.0001)	−0.33 (0.001)	−0.23 (0.03)
RASMB	−0.47 (<0.0001)	0.32 (0.01)	−0.44 (<0.0001)	−0.05 NS
RAVEG	−0.57 (<0.0001)	0.44 (0.0005)	−0.20 NS	−0.26 (0.02)
BTOL	−0.63 (<0.0001)	0.63 (<0.0001)	−0.41 (0.0001)	−0.06 NS
BINSECT	−0.23 (0.03)	0.11 NS	−0.23 (0.03)	0.32 (0.002)
BOMNI	−0.44 (<0.0001)	0.35 (0.006)	−0.48 (<0.0001)	0.18 NS
BINTOL	−0.48 (<0.0001)	0.29 (0.03)	−0.50 (<0.0001)	−0.16 NS
BTCARN	−0.40 (0.0001)	0.45 (0.0003)	−0.39 (0.0002)	−0.05 NS
IBI	−0.80 (<0.0001)	0.64 (<0.0001)	−0.61 (<0.0001)	−0.19 NS

effect of the degraded or inadequate habitat measured by the IBI that necessitates fish stocking. For example, Whittier et al. (1997) found lower cyprinid richness in lakes in the northeastern United States stocked with nonnative predators, but they also reported declines in cyprinid richness in the absence of predators when human activity in the watershed and along lake shorelines increased.

In this study, lakes in the NLF ecoregion had significantly higher IBIs than lakes in the CHF ecoregion. General physical features of the lakes in these ecoregions were similar, but average trophic state differed. There is evidence, however, indicating lakes in the CHF have undergone cultural eutrophication. A diatom core study showed many lakes in the CHF ecoregion were historically mesotrophic and became eutrophic post-European settlement, whereas lakes in the NLF ecoregion remained mesotrophic (Heiskary and Swain 2002; Ramstack et al. 2004). In addition, land use in the CHF region of Minnesota changed dramatically, from pre-European hardwood forests and prairie to modern day land use (row crop agriculture and urban), whereas forest cover is still the primary land use in the NLF ecoregion (Marschner 1930; Heiskary and Swain 2002).

The functional properties (i.e., trophic composition) of a lake may be more robust than structural properties (i.e., species richness). Schindler's whole-lake experiments have shown when large amounts of acid or nutrients are introduced into lakes, primary productivity and other aspects of community metabolism were remarkably homeostatic, but species composition of the plankton and fish were greatly altered (as cited in Odum 1985).

TABLE 9.—Coefficients of variation (100 × SD/mean) for metrics in the least disturbed lakes and disturbed lakes (lakes from all other land use groups pooled). Metric abbreviations are defined in Table 1.

Metric	Least disturbed (N = 16)	Disturbed (N = 73)
NAT	20	17
INTOL	21	75
TOL	47	106
INSECT	25	23
OMNI	45	78
CYP	55	48
SMB	43	62
VEG	24	45
BTOL	18	55
BINSECT	45	58
BOMNI	20	64
BINTOL	70	256
BTCARN	17	34
RAINTOL	69	142
RASMB	82	117
RAVEG	105	155

Margalef (1981) states that stress is something that puts into action the mechanism of homeostasis. Species replacement and other adjustments tend to keep the overall function of a system steady. As a result, the early warning of stress will be more easily seen at the species level. Once stress is detectable at the ecosystem level (functional level), there is real cause for alarm, for it may signal a breakdown in homeostasis. Metric responses in this study support these observations. Species richness-based metrics were more sensitive to degradation than trophic composition, the loss of sensitive species occurring at relatively lower levels of system stress. In addition, differences in metric

TABLE 8.—Extended.

Metric	Lakeshed (N = 51)		Buffer (N = 89)	
	PCA1_LS	PCA2_LS	PCA1_BF	PCA2_BF
NATIVE	−0.25 NS	0.12 NS	−0.14 NS	−0.28 (0.007)
INTOL	−0.61 (<0.0001)	0.15 NS	−0.49 (<0.0001)	−0.20 (0.06)
TOL	−0.39 (0.005)	0.12 NS	−0.43 (<0.0001)	−0.06 NS
INSECT	−0.28 (0.04)	0.08 NS	−0.34 (0.001)	−0.18 NS
OMNI	−0.26 NS	0.02 NS	−0.33 (0.001)	0.10 NS
CYP	−0.44 (0.001)	0.15 NS	−0.12 NS	−0.30 (0.005)
SMB	−0.37 (0.008)	−0.01 NS	−0.26 (0.02)	−0.07 NS
VEG	−0.39 (0.005)	0.15 NS	−0.41 (0.0001)	−0.20 NS
RAINTOL	−0.47 (0.0005)	−0.04 NS	−0.43 (<0.0001)	−0.04 NS
RASMB	−0.51 (0.0001)	0.14 NS	−0.30 (0.005)	−0.17 NS
RAVEG	−0.20 NS	−0.09 NS	−0.34 (0.001)	0.06 NS
BTOL	−0.52 (0.0001)	0.13 NS	−0.34 (0.0009)	−0.22 (0.03)
BINSECT	−0.45 (0.0009)	0.06 NS	−0.09 NS	−0.31 (0.003)
BOMNI	−0.66 (<0.0001)	0.08 NS	−0.23 (0.03)	−0.43 (<0.0001)
BINTOL	−0.59 (<0.0001)	0.16 NS	−0.36 (0.0006)	−0.22 (0.04)
BTCARN	−0.42 (0.002)	0.11 NS	−0.26 (0.02)	−0.27 (0.01)
IBI	−0.71 (<0.0001)	0.13 NS	−0.53 (<0.0001)	−0.29 (0.005)

TABLE 10.—The relative contribution of each metric expressed as the ratio of the variance of the differences between the full and reduced IBIs within a land use group and the variance of the differences over all lakes. Ratios greater than the group median (in bold italics) were considered potentially informative within that group. Metric abbreviations are defined in Table 1; see text for land use group abbreviations.

Metric	For1 (N = 16)	For2 (N = 14)	ForAg (N = 21)	AgUrbFor (N = 11)	Urb (N = 9)	Ag (N = 18)	Total variance
NAT	0.73	***1.08***	***0.99***	***1.18***	0.42	0.70	2.99
INTOL	0.31	0.66	***1.04***	0.78	***1.00***	***0.80***	6.78
TOL	***1.02***	0.65	***1.43***	***1.14***	0.27	0.78	6.64
INSECT	0.94	***1.54***	0.53	***1.19***	0.60	0.80	2.75
OMNI	0.94	0.46	0.94	0.88	0.72	***1.56***	6.69
CYP	0.89	***1.51***	***0.96***	***1.15***	0.65	0.68	8.24
SMB	***1.04***	1.02	0.69	0.72	***1.02***	0.76	6.22
VEG	***1.01***	0.38	***1.07***	***1.84***	***1.04***	***0.89***	4.11
RAINTOL	***1.18***	***1.12***	***1.68***	0.40	0.05	0.38	5.95
RASMB	***1.54***	***1.77***	0.45	***1.20***	0.91	0.42	6.32
RAVEG	***1.87***	***1.07***	***1.08***	0.22	0.07	0.66	7.50
BINSECT	0.49	0.74	0.91	0.79	***1.30***	0.33	7.91
BOMNI	0.29	***0.96***	***1.19***	0.67	***1.38***	0.80	7.43
BTOL	0.39	0.67	0.56	***1.51***	***2.01***	***1.52***	7.73
BTCARN	0.62	0.74	0.91	***1.78***	***1.07***	***1.33***	4.47
BINTOL	***1.75***	***1.15***	0.70	0.19	0.13	0.67	7.27

contribution among land use groups show trophic composition metrics were more informative in more-disturbed lakes, likely because trophic composition metrics were stable in less-disturbed lakes and did not begin to respond to stressors until stressor levels were relatively high.

Although localized disturbances have been shown to impact fish assemblages on a local scale (Poe et al. 1986; Bryan and Scarnecchia 1992; Jennings et al. 1999b), trophic status probably acts as a filter limiting the potential whole-lake species pool (Tonn 1990). Jennings et al. (1999b) found local habitat modifications lead to small changes in local species richness, but assemblage structure responded at larger spatial scales, when many diverse incremental changes have accumulated within a basin over time. Rose (2000) states that too much focus on a specific stressor alone can result in misleading predictions of responses to environmental quality because of inadequate information on how other factors affect the response of the population. Crowder et al. (1996) states the primary external controls on the nature and behavior of lake ecosystems are physical factors (water level changes, increased sedimentation), chemical factors (acidity, nutrients, contaminants), and the introduction of exotics. Furthermore, experience indicates changes in community structure induced by a primary stress may trigger secondary changes in other components of the ecosystem, even though the other species are not seriously or evenly directly affected by the primary stress (Crowder et al. 1996). Rose (2000) notes fish populations face multiple simultaneous stressors that cause simultaneous changes in environmental quality, and the cumulative effects of multiple stressors can differ greatly from the sum of their independent effects. In addition, it is difficult to identify responses to specific stressors because fish species have complex life histories, utilize different habitats during different life stages, and exhibit large interannual fluctuations in abundance (Rose 2000). Koonce et al. (1996) state that the diversity of a fish community, its structure, and its function depend on the availability of species that are capable of completing their life cycle within the lake ecosystem. These complex interactions prevent the detection of clear relationships between individual metrics and individual stressors. As Karr (1990) states, the complicated nature of biological systems makes traditionally defined risk assessment (i.e., a direct quantitative relationship between a hazard and its effect) inappropriate. The benefit of the IBI approach is that it allows a biologist to distill the biological meaning from large quantities of data into a single measure. This measure can then be used to compare biotic condition among lakes.

We envision two primary uses for the lake IBI. The first use would be for characterizing the current biotic integrity of lakes across Minnesota so that lakes that have maintained high biotic integrity are targeted for protection and lakes with diminished biotic integrity can be evaluated for potential restoration. Concerns that should be considered when using the IBI to characterize the current biotic integrity of a lake are natural metric variability and sampling noise, lag times in the response of the fish community to disturbances, and the potential existence of an extinction debt (Tilman et al. 1994). Because mechanisms (i.e., nutrient cycling, adaptive strategies of opportunistic species, and instability of substrates) that promote degradation can, after a certain point, become self reinforcing and create further degradation even after the source of the stressors are withdrawn (i.e., extinction debt), the most effective way to ensure healthy ecosystems is to limit stress so that self-reinforcing degradative processes are not set in motion (Rapport and Whitford 1999). Scheffer et al. (2001) note that building and maintaining resilience of the desired ecosystem state is likely the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change.

The second use for an IBI would be to measure the effectiveness of restoration efforts. This is more complicated. Water quality and habitat can be restored without a subsequent return of biotic integrity if species have been lost from the ecosystem. For this reason, habitat and water chemistry evaluations alone are inadequate assessments of biotic integrity. The presence of quality physical habitat or water chemistry does not guarantee the presence of a biota that is complete, healthy, and with integrity (Karr 1995). Unlike stream IBIs that usually measure the integrity of sections of streams and therefore have a potential upstream or downstream source of species for recolonization, once species are lost from a lake the chances of recovery are low. Even if a lake is connected to another lake, all lakes in an area are often subject to the same watershed level degradation. True restoration of biotic integrity may require actions that not only improve water quality and habitat but also include the reintroduction of lost species.

Acknowledgments

Thanks are extended to David Anderson, Leslie George, Michael Knapp, Mike McInerny, Jeff Reed, and Bill Thorn for assistance with data collection. Jack Wingate, Charles Anderson, Tim Cross, and David Anderson of the MNDNR critically reviewed this manuscript. This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell–Johnson) program.

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